

WOOD ANATOMY OF ONAGRACEAE: FURTHER SPECIES; ROOT ANATOMY; SIGNIFICANCE OF VESTURED PITS AND ALLIED STRUCTURES IN DICOTYLEDONS

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ABSTRACT

Quantitative and qualitative features are described for *Circaea lutetiana* subsp. *canadensis*, *Fuchsia decidua*, *Lopezia suffrutescens*, *Oenothera deltoides* subsp. *howellii*, and six species of *Ludwigia*. Comparison is made between secondary xylem of stem wood and that of tuberous roots for *Fuchsia decidua*; the roots have narrow, angular vessels with scalariform lateral wall pitting in a ground tissue of starch-rich parenchyma indistinguishable from ray cells. Succulent roots of *Xylonagra* show the same features. Wood anatomy for the species studied is interpreted in terms of habit and ecology; features relating to herbaceous modes of structure are discussed since all of the species studied can be termed subshrubs or small to large herbs. A discussion of the systematic distribution of vestured pits is presented. Allied phenomena (warted surfaces in conifer tracheids, warty surfaces in vessel elements some of which are intercontinuous with warts of vestured pits, grooves in vessel walls, and helical thickenings on vessel walls) are considered in conjunction with vestured pits. Experimental data available is minimal, so little evidence other than systematic distribution and occurrence within cell types can be adduced at present. These forms of wall relief seem to occur essentially only in conducting cells. Four hypotheses are entertained: (1), vestured pits as a means of preventing pit membrane rupture in pit aspiration; (2), wall relief as a means of lowering resistance to water flow; (3), wall relief as a mechanism for mending of air embolisms; and (4), wall relief as a means of increasing hydration (bonding of water to wall), thereby enabling high water tensions during drought or frost but lessening likelihood of cavitations. Although all hypotheses are considered possible in terms of today's limited knowledge, the fourth hypothesis is considered the most likely by virtue of systematic, ecological, and cell type occurrence of wall relief types.

Although a large assemblage of woods of Onagraceae have been covered in my two earlier studies (1975a, 1977), the availability of wood of additional species of interest prompts the present study. *Fuchsia decidua* Standl., a shrub of montane (ca. 2,000–3,000 m) Jalisco, Mexico, has semisucculent stems; its roots have swellings that suggest a storage function. This species offers an ideal opportunity to compare stem and root wood, but the roots are of a special type. Although stem wood of *Xylonagra arborea* (Kell.) Donn. Smith & Rose was studied earlier (1975a), liquid preserved material of the tuber-like roots in this plant was available for the present study. These roots offer an interesting comparison with the roots of *Fuchsia decidua*. Woods of *Lopezia* were sampled rather intensively (1975a), thanks to the excellent collections of Dr. Dennis E. Breedlove. One distinctive subshrub, *L. suffrutescens*, is added in the present study. *Lopezia suffrutescens* has numerous stems of short duration (one to several years) branching from the base of the plant. It offers interesting material on which to test the ideas enunciated earlier on the relationships between habit and interxylary phloem presence. *Lopezia suffrutescens* is a species restricted to canyons in Durango and Sinaloa (Plitmann, Raven & Breedlove, 1973).

Six species of *Ludwigia* are included here. The *Ludwigia* species in the earlier (1975a) study lacked interxylary phloem and had relatively mesomorphic

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woods. The species studied here offer material for additional information on these topics. The six *Ludwigia* collections studied here were made in marshy areas of Brazil by T. P. Ramamoorthy and P. M. Vital. Localities are as follows: *L. bullata* (Hassler) Hara, *Ramamoorthy & Vital 609*, Campo Grande, Matto Grosso; *L. elegans* (Camb.) Hara, *R.&V. 535*, Goiania; *L. peruviana* (L.) Hara, *R.&V. 598*, Banderante, Matto Grosso; *L. sericea* (Camb.) Hara, *R.&V. 642*, near Epitacio, Matto Grosso–São Paulo border; *L. tomentosa* (Camb.) Hara, *R.&V. 505*, Paracatu, Minas Gerais; *L. sp.* (aff. *L. longifolia*), *R.&V. 555*, Aereuna, Goias.

Two annuals included in the present study are *Circaea lutetiana* L. subsp. *canadensis* (L.) Asch. & Magnus (Antonia, Jefferson Co., Missouri) and *Oenothera deltoides* T.&F. subsp. *howellii* (Munz) Klein (Antioch, California). The genus *Circaea* has not been studied hitherto with respect to wood anatomy. Both of these annuals show changes in vessel diameter and density (and therefore change in xeromorphy) of wood over the course of a growing season. These patterns invite quantification and application to growth rings in woody plants.

The species included in the present study were assembled and transmitted to me through the kindness of Dr. Peter H. Raven.

The Onagraceae of the present study invite examination of special topics. One of these involves herbaceous modes of structure as exemplified in such respects as ray structure, a low (but not primitive) length ratio of imperforate tracheary elements to vessel elements, and the tendency for pits in walls of vessels to be laterally widened. A second topic of special interest involves vestured pits, which are characteristic of most Onagraceae. Vestured pits, distributed in a scattering of dicotyledon families, have not been easy for plant anatomists to interpret with respect to function. Vestured pits are considered here in a larger context, along with warted vessel and tracheid walls, grooving on vessel walls, and helical thickenings on vessel walls.

The anatomical data offered below for ten species of Onagraceae cannot be applied systematically on account of the fragmentary nature of these data. Those interested in applying wood anatomy to problems of systematics of Onagraceae will have to consult the earlier papers in this series (Carlquist, 1975a, 1977) as well as the summary of Vliet and Baas (1983) of wood anatomy of myrtalean families.

MATERIALS AND METHODS

The species provided to me by Dr. Peter H. Raven were all collected in the wild except for the tuberous roots of *Xylonagra arborea*, which were from a plant cultivated in greenhouses at the Missouri Botanical Garden. The material for this study includes one dried stem, that of *Oenothera deltoides* subsp. *howellii*, collected by Dr. John Thomas. The remaining material was provided in liquid-preserved form, pickled in formalin-acetic alcohol. Although *Oenothera deltoides* subsp. *howellii* had been included in an earlier (1975a) study, study of additional material of this taxon proved desirable. The stems provided of the *Ludwigia* were 1 cm or less in diameter; judging from the size of plants indicated in accompanying data (plants 2–3 m tall in *L. peruviana*, *L. sericea*, and *L. tomentosa*) the material supplied may not represent stems of maximal size for some of the species.

Wood of stems was sectioned on a sliding microtome; sections were stained with safranin. Wood of roots of the *Fuchsia* and the *Xylonagra* was embedded in paraffin; sectioned, without any form of softening, using a rotary microtome; and stained with a safranin-fast green combination; IKI was introduced as a starch stain.

ANATOMICAL RESULTS

Quantitative features are given for the ten species in Table 1. Both quantitative and qualitative features are presented in the descriptions of anatomical categories below and in the discussions of relationship between wood anatomy and ecology and plant habit.

Vessel elements.—The number of vessels per group in the species studied here (Table 1) falls within the range seen earlier in the family. This feature does not show significant variation within the family. Vessel diameter and vessel element length do vary significantly with species and are considered later with respect to ecology.

Vessels are rounded in outline in the species studied (Figs. 1, 11, 12, 15) with the notable exception of root wood of *Fuchsia decidua* (Fig. 6) and of *Xylonagra arborea* (Fig. 5). Vessels in these species are thin walled and narrow in diameter, but they are surrounded by parenchyma cells the same diameter as the vessels or larger. These circumstances probably result in the angular shape, as with species discussed earlier (Carlquist, 1975a, 1975b); within Onagraceae and other predominantly herbaceous families, angular vessels should not be interpreted as primitive.

Lateral wall pitting of vessels shows interesting variations in the present species. In *Circaea* (Fig. 13) and in the various species of *Ludwigia* vessels have pits round in outline, alternately arranged, on intervascular contacts; these two genera have alternate pits, elliptic rather than round, on vessel-parenchyma contacts. In the remaining species of the present study, pitting on vessels might be described as scalariform or pseudoscalariform (Figs. 7, 16). By this latter term I am designating patterns in which an alternate pattern intergrades with a scalariform pattern. Such a pattern is illustrated for stems of *Fuchsia decidua* (Fig. 9), but it was also observed on vessels of *Lopezia suffrutescens*. Vessel-ray contacts in the latter species showed pits with apertures notably wide, or "gaping." *Oenothera deltoides* subsp. *howellii* has all pits on vessels circular in outline.

Vestured pits may be found in all of the taxa presently at hand except *Oenothera deltoides* subsp. *howellii*; vesturing was reported absent in this taxon earlier (Carlquist, 1975a). Even when pits are wide and gaping (Fig. 7), vestures are present in vessels of roots in *Fuchsia decidua*. Possible functional interpretations of vestured pits are offered in a later section of this paper.

Tyloses were observed in vessels of roots of *Fuchsia decidua* (Fig. 7) and in stems of *Lopezia suffrutescens*.

Libriform fibers.—Nucleated libriform fibers occur in all of the species studied here (not visible in *Oenothera deltoides* subsp. *howellii* because that material was dried instead of preserved in liquid). In all of the species studied here, both libriform fibers with gelatinous walls and libriform fibers with ordinary lignified

TABLE 1. Wood characteristics of Onagraceae. (Continued on facing page.)

Species	Collection	1
<i>Circaea lutetiana</i> L. subsp. <i>canadensis</i> (L.) Asch. & Magnus	A. Christ in 1975 (MO)	1.68
<i>Fuchsia decidua</i> Standley	Breedlove 15821 (MO)	1.73
<i>Lopezia suffrutescens</i> Munz	Breedlove 24534 (MO)	2.10
<i>Ludwigia bullata</i> (Hassler) Hara	Ramamoorthy & Vital 609 (MO)	1.40
<i>L. elegans</i> (Camb.) Hara	R.&V. 535 (MO)	1.96
<i>L. peruviana</i> (L.) Hara	R.&V. 598 (MO)	1.16
<i>L. sericea</i> (Camb.) Hara	R.&V. 642	1.24
<i>L. tomentosa</i> (Camb.) Hara	R.&V. 505	1.28
<i>L. sp.</i> (aff. <i>L. longifolia</i>)	R.&V. 555	1.20
<i>Oenothera deltoides</i> T.&F. subsp. <i>howellii</i> (Munz) Klein	J. Thomas	2.11

Legend for Table 1: 1, mean vessels per group. 2, vessels per mm², mean. 3, mean vessel diameter, μm . 4, mean vessel element length, μm . 5, mean libriform fiber length, μm . 6, mean libriform fiber diameter at widest point, μm . 7, mean libriform fiber wall thickness, μm . 8, mean multiseriate ray height, μm . 9, mean uniseriate ray height, μm . 10, ratio of libriform fiber length to vessel element length. 11, vulnerability ratio (vessel diameter divided by vessels per mm²). 12, mesomorphy ratio (vulnerability ratio multiplied by vessel element length). Where more than one figure is shown in columns 2, 3, 11, and 12, the figure before slash = earlywood, figure after = latewood. Means based on 25 measurements.

walls were observed. Gelatinous fibers may be seen above in Fig. 12 and Fig. 15, ordinary fibers below in the same photographs.

Axial parenchyma.—The present species agree with Onagraceae described earlier in having scanty vasicentric parenchyma, limited to a few cells around vessels. However, in roots of *Fuchsia decidua* (Figs. 3, 4, 6) and *Xylonagra arborea* (Fig. 5), axial parenchyma is present instead of libriform fibers. This parenchyma is rich in starch (Figs. 6, 7, 8); some of the grains are compound. The parenchyma cells are much larger in diameter than libriform fibers; longitudinally they are relatively short (Fig. 4) and may represent subdivision of a fusiform initial derivative into perhaps three cells, but the adult cells are not clearly grouped into strands. The axial parenchyma cells in these roots cannot be distinguished from ray cells in a tangential section.

Vascular rays.—Rays in all of the taxa studied here are predominantly uniseriate (Figs. 2, 14, 17). Biseriate or pluriseriate rays are so scarce in some of the taxa that figures for multiseriate ray height were not included for them in Table 1. Ray cells have lignified walls except in the roots of *Fuchsia decidua* (Figs. 3, 4, 6) and *Xylonagra arborea* (Fig. 5). Notably short rays occur in *Oenothera deltoides* subsp. *howellii* (Table 1). Rays consist of upright cells predominantly in all of the species studied except for *Oenothera deltoides* subsp. *howellii*, in which procumbent cells were seen. No square or procumbent cells were seen in rays of *Circaea lutetiana* subsp. *canadensis* (Fig. 14).

Interxylary phloem.—In my 1975a study, the three species of *Ludwigia* studied all lacked interxylary phloem. In the present study, of the six *Ludwigia* species only *L. sericea* has interxylary phloem (Fig. 11). It occurs as bands of various tangential extent near the periphery of the secondary xylem in the stem studied. Relatively large stems were supplied in this species. Interxylary phloem was absent in the collection studied of *Oenothera deltoides* subsp. *howellii*, whereas it was present in a collection of this species studied earlier (Carlquist, 1975a).

TABLE 1. Continued.

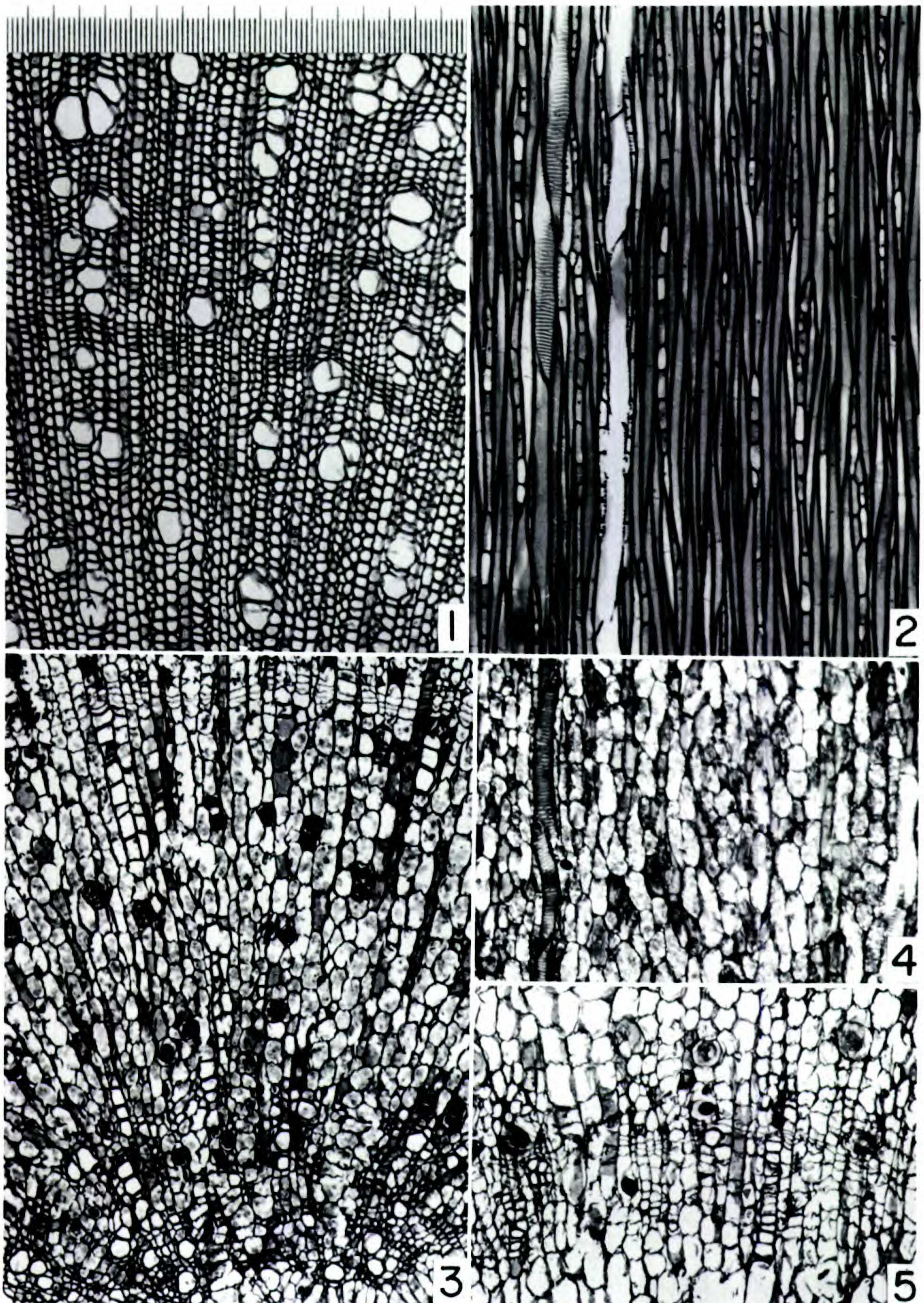
2	3	4	5	6	7	8	9	10	11	12
199/277	39/24	405	541	17	2.5	—	523	1.34	0.20/0.09	79/36
56	70	432	615	29	2.4	942	543	1.42	1.25	451
96	36	457	538	21	3.7	—	205	1.18	0.37	171
63	54	586	806	21	2.9	3478	863	1.38	0.85	500
71	52	483	747	19	3.3	1654	652	1.55	0.73	355
58	55	595	832	22	4.3	2832	1935	1.40	0.94	560
79	55	419	688	16	3.5	1896	903	1.64	0.69	291
92	51	495	791	17	3.3	3060	1235	1.61	0.56	278
130	40	491	697	19	3.5	2596	1364	1.42	0.31	151
37/61	58/37	234	316	10	2.5	210	78	1.35	1.65/0.64	386/149

Crystals.—Raphides were observed in axial parenchyma cells of *Fuchsia decidua* stems (Fig. 10). In roots of this species, cells bearing raphides occur idioblastically (Fig. 8) or in vertical pairs in the axial parenchyma that substitutes for libriform fibers. Rhomboidal crystals were observed to occur singly in ray cells of *Ludwigia bullata* and *L. peruviana*. Such crystals were reported for *Ludwigia octovalvis* (Carlquist, 1975a).

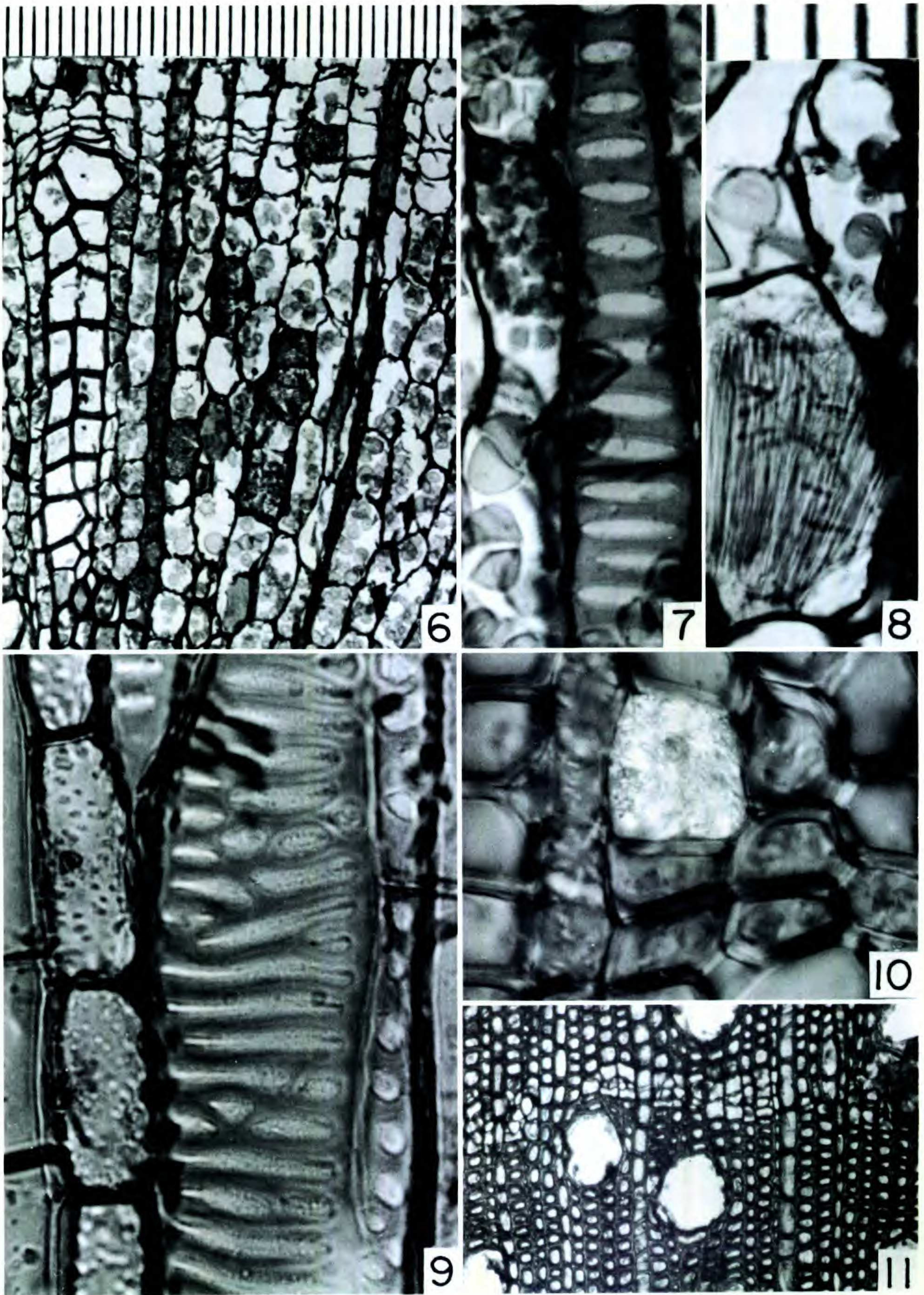
Starch; gummy deposits.—Onagraceae commonly contain starch in wood cells; starch was especially abundant in the material of *Fuchsia decidua* roots and stems (Figs. 3, 4, 6, 7, 8). Although not illustrated for stems, starch is abundant in this species in libriform fibers. Starch in libriform fibers was observed in *Lopezia suffrutescens*. In *Ludwigia elegans* and *L. peruviana*, starch was abundant in the libriform fibers, which are commonly septate. Dark-staining gummy compounds were observed in ray cells of *L. elegans*, *L. peruviana*, and *L. tomentosa*.

CORRELATIONS WITH HABIT AND ECOLOGY

Roots.—The succulent roots of *Fuchsia decidua* and *Xylonagra arborea* show a number of interesting modifications of xylary patterns. Vessel elements are few; they are quite infrequent up to the outermost xylem in the plants studied. In the outermost xylem (Figs. 3, 5, 6) vessel elements are present. They are narrower than stem vessels (compare Figs. 1 and 3) and tend to be grouped into radial rows (Fig. 6). The vessels are angular in transectional outline, a condition that should be interpreted not in terms of primitiveness but in terms of the fact that the vessels are narrow and surrounded by cells which are few in number and wide (see Carlquist, 1975a, 1975b). The horizontal width of pits (scalariform or nearly so) and the gaping nature of pit apertures (Fig. 7) suggest that vessels are exhibiting relaxed selection for mechanical strength, in accordance with my considerations on pedomorphosis (1962, 1975b). Also persuasive of relaxed selection for mechanical strength is the substitution of parenchyma for all libriform fibers. Starch is stored abundantly in the root parenchyma of *Fuchsia decidua* and *Xylonagra arborea*; starch is also stored in the stems of *Fuchsia decidua*. The large dimensions of parenchyma cells in the roots of *Fuchsia decidua* and *Xylonagra*



FIGURES 1-5. Wood sections of *Fuchsia* and *Xylonagra*.—1-4. *Fuchsia decidua* Standley, *Breedlove 15821* (MO).—1. Transection of stem wood, showing vessels large in diameter compared to libriform fibers.—2. Tangential section of stem; rays narrow, mostly uniseriate.—3. Transection of root; pith below, cambium above.—4. Tangential section of root; vessel at left; all other xylem is parenchyma with rays indistinguishable from axial parenchyma.—5. *Xylonagra arborea* (Kell.) Donn. Smith & Rose, H. Towner in 1969 (MO). Transection of root, showing later-formed xylem; cambial zone, center; most of wood is parenchyma. Figs. 1-5, scale above Fig. 1 (finest divisions = 10 μ m).



FIGURES 6-11. Wood sections of *Fuchsia* and *Ludwigia*.—6-10. *Fuchsia decidua*, Breedlove 15281 (MO).—6. Transection of root, showing radial grouping of angular vessels, left; cambial zone above.—7. Portion of tangential section of root; vessel shows vessel-parenchyma pitting; starch grains, left.—8. Portion of tangential section of root; starch grains above, raphides below.—9. Portion of tangential section of stem; vessel pitting is alternate with tendency toward scalariform.—10. Portion of transection of stem; light polarized to show raphides in axial parenchyma cell.—11. *Ludwigia sericea* (Camb.) Hara, Ramamoorthy and Vital 642 (MO), transection of outer portion of stem wood cylinder, showing a band of interxylary phloem. Figs. 6, 11, scale above Fig. 6 (divisions = 10 μ m). Figs. 7-10, scale above Fig. 8 (divisions = 10 μ m).

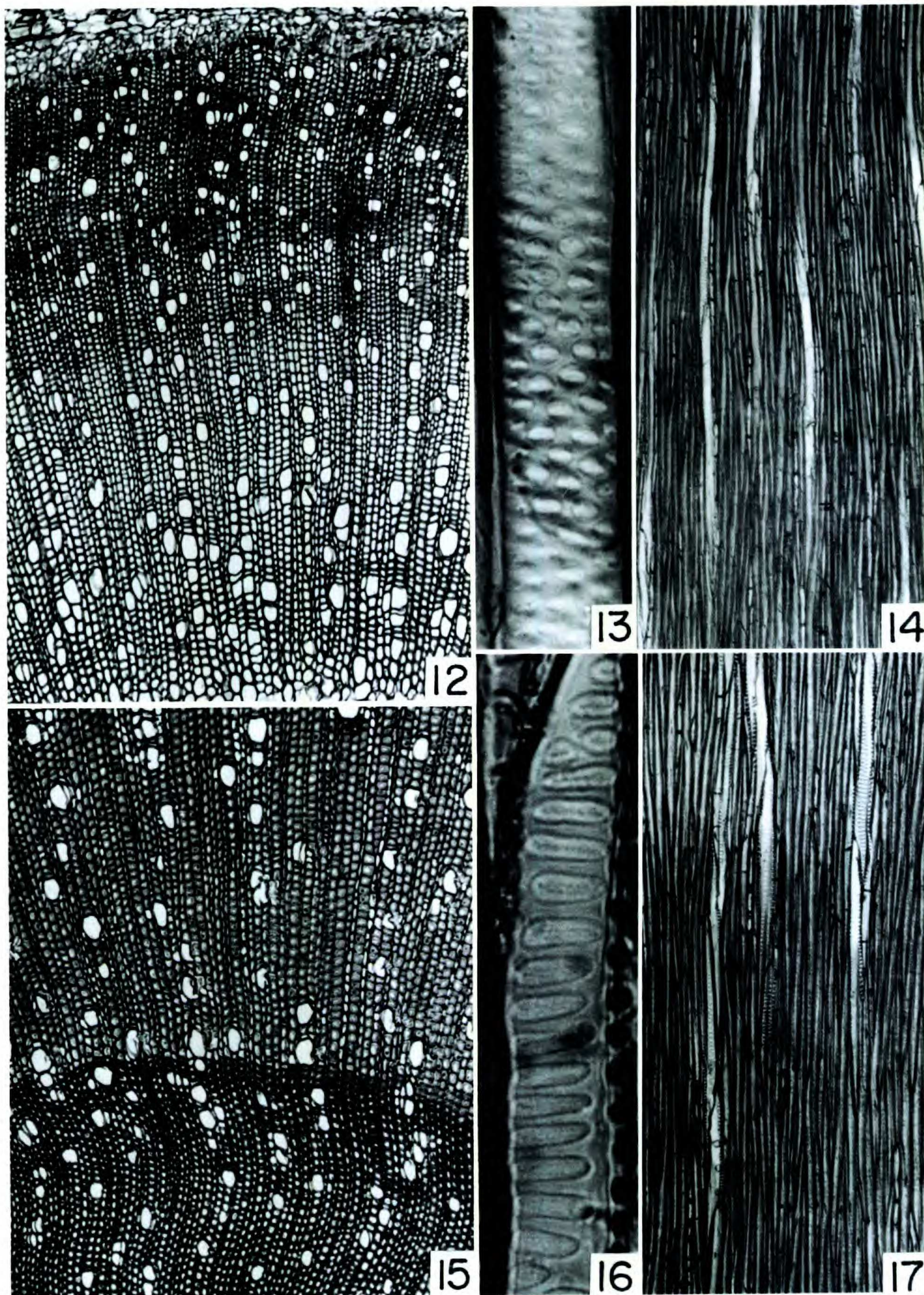
arborea seem clear indications that these roots serve for water storage also. The deciduous habit of *F. decidua* seems to confirm a water storage capability.

Herbaceousness.—The rather large pit apertures of vessel elements of *Lopezia suffrutescens* (Fig. 16) may relate to moderate selective pressure for mechanical strength; this species has only small stems. *Lopezia suffrutescens* also has relatively short libriform fibers. The low length ratio between libriform fibers and vessel elements in this species (1.18) is notable. In woody dicotyledons, a low ratio of this kind would indicate primitiveness; in a specialized group of herbs, it probably does not. Indeed, annual Onagraceae tend to have lower values for this ratio than trees or shrubs in the family (Carlquist, 1975a). The scalariform pattern of vessel pitting in *L. suffrutescens* (Fig. 16) may be said to be derived, in formal terms, by extension of metaxylem patterns into the secondary xylem, “paedomorphosis” (Carlquist, 1962). In functional terms, one may say that the metaxylem has low mechanical strength (there is often compensation in the form of collenchyma or, later, extraxylary fibers in the stem, or addition of libriform fibers as secondary growth commences). One may also say that secondary xylem of herbs which resembles metaxylem in vessel pitting shows relaxed selection for mechanical strength (Carlquist, 1975b).

The lack of procumbent cells in rays in most of the Onagraceae studied here could be related to herbaceousness, for subdivision of ray initials takes place over time, as pointed out by Barghoorn (1941) and stressed by numerous subsequent authors. This would account especially for the lack of square or procumbent cells in wood of *Circaea lutetiana* subsp. *canadensis*. The wood of another annual, *Oenothera deltoides* subsp. *howellii*, does have procumbent cells in rays; in this taxon, however, stems are much larger, so there is more potential opportunity for horizontal subdivision of ray initials to occur. Within the Onagraceae sampled here, rays appear to be mostly or exclusively uniseriate as secondary growth begins. This condition, however, is not necessarily related to herbaceousness at all, and may be found in a scattering of dicotyledons, such as *Illicium* (Carlquist, 1982a) and *Sarcococca* (Carlquist, 1982b).

Mesomorphy and xeromorphy.—Narrow vessels, more numerous vessels per mm² of transection, and short vessel elements prove to be indicators of xeromorphy (Carlquist, 1975b). These three features are apparently related to three different physiological characteristics, and therefore are not redundant; the three conjunctively are reliable as indicators, just as each alone is (Carlquist, 1982a).

Vessel diameter shows fluctuations within a stem. This is most obvious in the case of growth rings. However, wood of an annual (which might be likened to a single growth ring) also shows vessel diameter fluctuations. Vessels are wider and fewer per mm² at the beginning of secondary growth. This pattern is shown by both *Circaea lutetiana* subsp. *canadensis* (Fig. 12) and *Oenothera deltoides* subsp. *howellii*. Consequently, both early and late season figures have been computed for wood of these two species in Table 1. Using the vulnerability and mesomorphy indices as devised earlier (Carlquist, 1977), one can see that there is appreciably more mesomorphy at the beginning of a growth ring than at the end, assuming no change in length of vessel elements (measurements on length of vessel elements using radial sections of the two annuals showed no change in vessel element length). Certainly shift in vessel diameter and density would be



FIGURES 12-17. Wood sections of *Circaea* and *Lopezia*.—12-14. *Circaea lutetiana* L. subsp. *canadensis* (L.) Asch. & Magnus, A. Christ in 1975.—12. Transection; pith below, cambium above; vessel diameter decreases.—13. Vessel element from tangential section, pits alternate.—14. Tangential section, rays all uniseriate, ray cells all erect.—15-17. *Lopezia suffrutescens* Munz, Breedlove 24534 (MO).—15. Transection; dark zone below center delimits first from second year's xylem.—16. Vessel from tangential section, showing scalariform vessel-parenchyma pitting.—17. Tangential section, showing sparse uniseriate rays. Figs. 12, 14, 15, 17, scale above Fig. 1. Figs. 13, 16, scale above Fig. 8.

ways of accommodating xeromorphy more easily than shortening of vessel element length; the latter change requires alteration of a deep-seated feature, length of the fusiform cambial initials. A number of groups show shift to wood xeromorphy by narrowing of vessels and increase in vessel density without change in vessel element length (Carlquist, 1982a, 1982b). One may say that in the case of *Circaea lutetiana* subsp. *canadensis*, the very low vulnerability ratio for end-of-season wood (0.09) is comparable to vulnerability ratios for desert plants, whereas the ratio early in the season (0.20) is only moderately xeromorphic. Shifts of this nature in the wood of an annual suggest that analysis of earlywood and latewood separately with respect to both vulnerability and mesomorphy ratios would be valuable for woody species with growth rings. Such analysis could demonstrate quantitatively precisely to what degree earlywood and latewood are mesomorphic or xeromorphic. However, even when earlywood and latewood are combined for the purposes of developing figures for vulnerability and mesomorphy in a species, comparison of species so analyzed can demonstrate how very sensitively these ratios reflect demonstrable ecological differences among species (Michener, 1981).

In species of *Ludwigia* analyzed earlier (Carlquist, 1975a), vessel elements did not seem exceptionally mesomorphic in terms of vessel diameter or density, but the length of vessel elements did seem to indicate mesomorphy for the genus as a whole. The same quantitative features are present in the six species of *Ludwigia* studied here. Paedomorphosis (Carlquist, 1962) could be used as an explanation of how relatively long vessel elements can occur in *Ludwigia*, which is a group of small to large herbs quite unlike the woody types (with relatively long vessel elements) likely to have been ancestral in the family, judging from woods of *Hauya* and *Fuchsia* (although certainly other features of those two genera are not primitive within the family).

Interxylary phloem.—In the initial study of this series (Carlquist, 1975a), distribution of interxylary phloem within Onagraceae was discussed. One criterion for presence or absence was claimed to be constituted by rapidity and seasonality of photosynthate storage and mobilization. Interxylary phloem is absent in Onagraceae with an almost continuous pattern of growth. It tends to be present in those genera and species in which growth and flowering occur suddenly and seasonally, and in which flowering and fruiting represent presumptively large energy expenditures. A second correlation cited for presence of interxylary phloem was stem size. Where stems are larger, the occurrence of one or more bands of interxylary phloem is more likely. The species in the present study lack interxylary phloem except for *Ludwigia sericea*. In the earlier study, the three species of *Ludwigia* examined lacked interxylary phloem. In *L. sericea*, stems are among the larger of the species in this genus examined; the bands of interxylary phloem occurred only near the periphery of the stem studied. These circumstances seem to validate the correlation between stem diameter and interxylary phloem. Likewise, *Lopezia suffrutescens* is informative, but in a different way. In the earlier survey, the only taxon within *Lopezia* that lacked interxylary phloem was one with relatively small stems, *L. racemosa* subsp. *racemosa*. In the present study, *L. suffrutescens* proved to lack interxylary phloem; the stems of this species are of short duration, related to the subshrub habit of this plant. However, no single

factor controls production of interxylary phloem, and in order to understand the correlations of interxylary phloem occurrence within groups where it is both present and absent, as in Onagraceae, we must take into account habit, seasonality, and massiveness of flowering and fruiting. Even then, general but not precise correlations will likely result.

SIGNIFICANCE OF VESTURED PITS AND ALLIED STRUCTURES IN DICOTYLEDONS

Vestured pits have been listed for the myrtalean families Combretaceae, Crypteroniaceae, Lythraceae, Melastomaceae, Myrtaceae, Oliniaceae, Onagraceae, Punicaceae, and Sonneratiaceae by Bailey (1933) and Metcalfe and Chalk (1950). Vestured pits also occur in the myrtalean family Penaeaceae (Carlquist & DeBuhr, 1977). Other families possessing vestured pits listed by Bailey and by Metcalfe and Chalk are Apocynaceae, Asclepiadaceae, Brassicaceae, Cappara-ceae, Dipterocarpaceae, Euphorbiaceae, Fabaceae, Loganiaceae, Malpighiaceae, Ochnaceae, Oleaceae, Polygonaceae, Rubiaceae, Thymeleaceae, and Vochysi-aceae. Additional families in which vestured pits have been reported in recent years include Boraginaceae (Carlquist, 1970; Miller, 1977), Cistaceae (Baas and Werker, 1981), Gonystylaceae (Scurfield, Silva & Ingle, 1970), Proteaceae (Meylan & Butterfield, 1974), and Sarcolaenaceae (Baas & Werker, 1981). However, as is clear from Meylan and Butterfield (1974, 1978), the warts that comprise vestures are not restricted to the pits, but may be present both within pit cavities and also spread over walls of a vessel in such species as *Leptospermum ericoides* A. Rich., *Metrosideros robusta* A. Cunn., and *Persoonia toru* A. Cunn. This is also illustrated for two species of *Bourreria* (Boraginaceae) by Miller (1977). Also, there are examples of dicotyledon species in which warts like those in vestured pits occur on vessel walls but not within the pits themselves: *Fagus grandifolia* Ehrh., *F. orientalis* Lipsky, *F. sylvatica* L., *Platanus occidentalis* L., and *Sassafras albidum* (Nutt.) Nees. (Parham & Baird, 1974). Warded vessel walls were claimed to be part of the same phenomenon as vesturing morphologically by Coté and Day (1962), and evidence to this effect has continued to mount (Scurfield & Silva, 1970). The visual appearance of warded vessel walls and vestured pits in such species as *Leptospermum ericoides* and *Persoonia toru* (Meylan & Butterfield, 1974, 1978) is very persuasive in this regard.

If one is to include instances of warded walls, one must note that the majority of conifer woods have a warded layer (Kobayashi & Utsumi, 1951; Liese, 1951). Vessels in Gnetaceae have vestured pits (Bailey, 1933). Tracheids of Winteraceae have a warty layer much like the warty layer of conifers (Meylan & Butterfield, 1978). Warts like those on tracheid walls but too small to appear as typical vesturing occur within the pit cavities of conifer tracheids (Meylan & Butterfield, 1978).

I would like to draw attention to patterns formed by these groups. In addition, one must note that vestured pits may occur not only on vessel elements in a species, but also on tracheids in the same wood: for example, in *Alstonia* of the Apocynaceae and in *Gonystylus* of the Gonystylaceae (Scurfield, Silva & Ingle, 1970). Illustrations of this condition are offered by Meylan and Butterfield (1978)

for *Metrosideros* (Myrtaceae). One may find vesturing on vessel pits in families that lack vesturing on imperforate elements, but in many cases those imperforate tracheary elements prove to be libriform fibers (e.g., Boraginaceae, Fabaceae, Onagraceae, Rubiaceae), which can be regarded as cells not genuinely part of the "conducting system." Much remains to be learned about to what extent fiber-tracheids and tracheids in dicotyledons have vested pits in those families where vessels have been observed to have vested pits. However, Bailey's (1933) generalization that vested pits relate to the conductive cells does appear to be, in general, validated as studies in electron microscopy improve our knowledge. The genera cited as exceptions to this principle by Scurfield, Silva and Ingle (1970)—*Alstonia* and *Gonystylus*—are, as noted above, genera in which tracheids, not libriform fibers, are the imperforate cell type and therefore vested cells are still part of the conducting system rather than the mechanical system.

Warts allied in appearance to vestures have distributions that prove to be very curious and interesting. Parham and Baird (1974), on the basis of a very limited sample, thought that angiosperms with scalariform perforation plates might have warty vessel walls more frequently than angiosperms with simple perforation plates. If one reviews a larger assemblage of species (e.g., Meylan & Butterfield, 1974), one sees that this is not true. However, the correlation between wartiness of vessel walls and position of vessels within a growth ring reported by Parham and Baird (1974) is worth consideration. These authors found latewood (but not earlywood) vessels to be warted in *Fagus grandifolia*, *F. orientalis*, and *Sassafras albidum*. Ohtani and Ishida (1973) reported a similar distribution of warted walls within growth rings of *Fagus crenata* Blume.

There is a parallel to the conditions mentioned above in the tendency for helical thickenings and helical sculpture to be more prominent in latewood vessels than in earlywood vessels. Such a pattern can be seen in Asteraceae, for example. Also, one may note that in angiosperms, helical thickenings and helical sculpture occur in vessels and vascular tracheids, but not in libriform fibers (exceptions may perhaps be found, but seem not likely to bulk large). Thus, the distribution of helical thickenings is like the distribution of warted surfaces. Not all conifer tracheids have helical thickenings, but some characteristically do. A few angiosperm taxa have both helical spirals and vested pits (e.g., *Coprosma arborea*, Meylan & Butterfield, 1978), but bulk rather small compared with the number of species that have helical sculpture but no vesturing on vessel pits. Helical sculpture has a systematic and ecological distribution which is not easy to interpret. Are forms of helical sculpture at all comparable to presence of warts on vessel walls?

We may construct a series of hypotheses for the functions of vested pits, warts, and—if allied in nature—helical sculpture. In constructing such hypotheses, one must concede that vested pits do not evolve in each species for which vested pits are positively adaptive by virtue of a physiological or ecological situation. Likewise, vested pits will not disappear immediately when a phylad evolves into an ecological condition where vested pits are not positively adaptive—the genetic information for their formation cannot be erased immediately. If one interprets vested pits as adaptive in Myrtales because of resistance of these structures to some factor involved in xeric conditions, evolution of some

portions of this order into moist conditions (e.g., *Fuchsia*) is not necessarily accompanied by loss of vestures, at least over short periods of geological time. Also, vascular plants have a multiplicity of devices for dealing with water relations: in some plants vessel numbers and dimensions might alter to confront ecological situations, in other plants leaf anatomy might be an effective device, while in yet others physiological pathways (crassulacean acid metabolism) or deciduousness of leaves might be invoked.

Conceding these evolutionary curricula, one may construct the following hypotheses:

1. Vestured pits can be supposed to prevent excessive deflection and rupture of pit membranes when there is a greater tension on one side of a pit membrane than on the other. This hypothesis was suggested by Zweypfenning (1978), who notes that vestured pits occur in some groups of dry situations. He seems to doubt his own hypothesis because presence or absence of vestured pits does not follow ecological conditions precisely. Although one cannot rule out Zweypfenning's hypothesis on the basis of presently available data, one must note that it does not explain instances where warts are present on vessel walls but not in pits (which are thereby vestured), nor does it explain warted borders on coniferous pits or warted inner surfaces of conifer tracheids.

2. Vestured pits and warted walls could be hypothesized to have lowered resistance to water flow. Such a hypothesis would be in line with the experiments of Jeje and Zimmermann (1979), who found that helical thickenings on vessel walls lower flow resistance as much as 40%. Such a hypothesis would subsume that all forms of relief on vessel walls would result in more rapid water flow. More importantly, such a hypothesis would assume that lessened resistance to water flow is the operative selective factor, rather than some other capability of the various forms of wall relief. Certainly simpler methods of achieving lowered resistance to water flow (e.g., wider vessels) can be envisaged. However, one may question whether the lowered resistance to water flow is the most important effect of helical sculpture presence (Carlquist, 1980). Woods rich in helical sculpture of vessels tend to occur in drier habitats (Webber, 1936; Carlquist, 1966; Michener, 1981); these species tend to have presumptively lower transpiration rates (they usually have much curtailed leaf surface) so that rapidity of flow, if that is what lowered flow resistance achieves, may not be a factor of prime selective importance. If one looks at geographical and ecological distribution of taxa in which species with and without helical sculpture occur, one sees that not only dry conditions but also frost likelihood is correlated with occurrence of helical sculpture presence (Carlquist, 1982a, 1982b). As with dry conditions, reduction of flow resistance may not be of major selective importance where frost occurs.

3. One could hypothesize that various forms of wall relief in conductive cells are mechanisms for eliminating air cavitations in vessels and tracheids and restoring normal water columns. Our ideas on how air embolisms, once formed, may be reduced are quite uncertain at the present time. I know of no data to support the idea that wall relief could function in this fashion. One could note that monocot-

yledons lack vestured pits, warted wall surfaces, and helical sculpture manifestations to a considerable degree, and that by virtue of root pressure, monocotyledons (even palms) can clear embolisms out of their vessels. While vestured pits and helical sculpture are characteristically absent from monocotyledon xylem (and from many but not all dicotyledonous vines), lack of high tensions in conductive systems may be of significance in analyzing absence of wall relief. In any case, more specific kinds of information are needed before we can consider further the idea that wall relief might be related to reduction of air cavitations in xylem.

4. One can hypothesize that vestured pits, warts, and helical sculpture increase surface area and therefore increase bonding of water molecules (hydration) to the cell surface. This, in turn, would have the effect of permitting water columns to withstand higher tensions without breaking: either the water columns in the tracheids and vessels themselves, or the portions of water columns in the pit cavities. This hypothesis would explain the presence of vestured pits (or warted pit cavities in conifers) by saying that pits represent the sites most likely to be points of entry for air bubbles under conditions of high tension. By localization of high hydration characteristics at pit cavities, the entry of air embolisms would be most effectively countered. Where relief is distributed over the entire wall (helical sculpture, grooves, warts), heightened hydration would be characteristic of an entire conducting cell, and the tension such a cell could sustain would be higher. Conducting cells with any of these forms of relief could be expected where ecological conditions of drought or physiological drought (frost, freezing of groundwater) occur. This would explain known patterns of wall relief distribution. For example, the frequency of helical sculpture is higher in species from dry areas (Webber, 1936; Carlquist, 1966) and colder areas (Carlquist, 1982a, 1982b). The warted nature of latewood as compared to non-warted earlywood in species cited earlier would also represent an interesting correlation: water tension would be higher in latewood than in earlywood.

I tend to feel that this fourth hypothesis, sketched elsewhere (Carlquist, 1982a) but elaborated here, can be supported by more numerous examples from systematic and ecological distribution of wall relief in conducting cells than can the other hypotheses at present. However, one must keep in mind that more than one tool is available to the plant in dealing with water relations. Also, any particular form of wall relief (e.g., vestured pits) must have had multiple origins if one can judge from systematic distributions. Thus, for example, in a particular locality one might find coexisting a conifer with warted tracheid walls, a legume with vestured pits in vessels, a composite with helically sculptured vessels, and a stem succulent with no relief at all on vessels. In this latter connection, one may note that forms of helical relief do happen to be infrequent, as far as we know, in stem or leaf succulents, where succulence rather than xylem anatomy is a prime tool for dealing with water relations.

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